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EXTENT OF DOUBLE-BROODING AND SEASONAL MOVEMENT OF NESTING FEMALES IN A NORTHERN POPULATION OF WOOD THRUSHES

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ABSTRACT.—Accurate estimates of the amount of double-brooding within a population are an important parameter for assessing the population sustainability of forest birds. In 1998 and 1999, we color-banded adult female Wood Thrushes (*Hylocichla mustelina*) at 70 nests early in the breeding season to assess the frequency of double-brooding in a northern population. We found that double-brooding was a common breeding strategy among Wood Thrushes in southern Ontario. Forty-seven females fledged first broods and 74% (n = 35) of them initiated egg-laying in a subsequent nest. It is possible that at least 87% (n = 41) of the females were double-brooded, based on the evidence of 6 later nests built within 50 m of successful first nests that were depredated or fledged young before their owners could be identified. Other second-brood nests were probably missed because they were overlooked and because some females moved considerable distances (100–400 m) between nestings. Most birds that failed in their early nesting attempt were not found again on the site, precluding verification of their renesting efforts. *Received 3 April 2000, accepted 4 August 2000.*

Wood Thrushes (*Hylocichla mustelina*) typically raise two broods annually in the southern part of their North American breeding range (Roth et al. 1996) but the number of broods normally produced in northern populations is unclear. It might be supposed that Ontario populations would have second broods less often than populations at more southerly latitudes where nesting may begin as much as a month earlier (Roth et al. 1996). Nevertheless, the literature on other northern populations of Wood Thrushes often refers to the species as double-brooded (i.e., females making a subsequent nesting attempt after fledging a first brood) although documentation is sketchy (Peterjohn and Rice 1991) or relies on information gathered from other, more southerly locales (Pinkowski 1991, Donovan et al. 1995).

In southern Ontario, the extremes of egg dates have been used as a gauge of probable Wood Thrush double-brooding (Peck and James 1998). However, egg dates at similar latitudes in Vermont suggest that double-brooding is infrequent in that region (Kibbe 1985). A problem with using egg dates as an indicator of double-brooding is that they fail to distinguish between actual second brooding attempts and replacement efforts following failure.

A clear understanding of the amount of double-brooding within a population is needed to accurately assess productivity and population viability, an important exercise particularly for Wood Thrushes, which have recently declined over large portions of their breeding range (Sauer et al. 1999). Models of northern Wood Thrush populations have assumed that all females are double-brooded if their first nest succeeds (Donovan et al. 1995, Friesen et al. 1999). However, if the frequency of double-brooding is overestimated, these models overestimate the reproductive output of a population and wrongly conclude that it is a source rather than a sink. The potential importance of double-brooding to estimates of population viability is reflected in the examples of Wood Thrushes and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) in southern Ontario. Both species have similar rates of nesting success (ca 50%) but because thrushes were considered to be double-brooded and grosbeaks single-brooded, the former but not

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the latter was classified as self-sustaining (Friesen et al. 1999).

We designed a study to validate some of the assumptions used in population modeling of northern Wood Thrushes. Our primary objective was to assess the amount of double-brooding in a population of color-banded birds by tracking individuals and their nests through two breeding seasons. We also investigated the movement of females within the breeding season, whether they remained on site regardless of nesting outcome, and whether all their nests were located in the same general vicinity.

STUDY AREA AND METHODS

Study sites.—Field research was conducted in two regions 50 km apart in southwestern Ontario (43° N, 80° W); Waterloo Region, a fragmented agricultural landscape with 14% forest cover (see Friesen et al. 1999 for a general description of the landscape) and the Niagara Escarpment, an area with 48% forest cover (Ramsay 1996). Wood Thrushes were studied in seven woodlands (sized 2, 4, 8, 10, 18, 24, and 140 ha) in Waterloo Region and three woodlands (sized 20, 20 and 1200 ha) on the Niagara Escarpment. Three sites in Waterloo were clustered together and separated 50–150 m by a highway and a cornfield. The remaining sites in both regions occurred singly and were separated from each other by at least 1 km. Primary habitat at all sites was upland deciduous forest dominated by sugar maple (*Acer saccharum*) with smaller amounts of white ash (*Fraxinus americana*) and American beech (*Fagus grandifolia*).

Data collection.—An intensive nesting and banding study was conducted from mid-May through August in 1998 and 1999 (see Friesen et al. 1999 for a full description of nest searching and monitoring techniques). We attempted to find all nests within each of the woodlands, except the largest forest in each region, using three to six person search teams. In the two large forests, only about a 30 ha section in each could be effectively searched because of time and logistical constraints. Nest searches were conducted at each site at least once a week (on average a minimum of 20 person hours per site per week) throughout the breeding season.

We captured and color banded as many nesting female Wood Thrushes as possible throughout the breeding season using two mist nets positioned in an L-shape within 15 m of active nests. We did not attempt to capture birds in cold or rainy weather and closed the nets for the day if birds were not captured within 1.5 hours. Captured birds were weighed, measured, sexed (Pyle 1997), and fitted with a unique combination of three plastic color bands and one numbered aluminum band. To find second broods, nest searching was intensified around the nests of banded birds that had earlier fledged young. Banded females were classified as double-brooded if they fledged at least one host young from an early nest and initiated egg laying in a subsequent nest.

We modified our capture protocol slightly in the second year of study. In 1998, because of concern over nest disruption, we attempted to capture adult females only after the eggs had hatched. In 1999, we began netting birds as soon as the clutch was complete to improve our chances of confirming double-brooded birds. Our change in capture timing did not seem to negatively impact nesting success; there was no incidence of nest desertion even though many females were captured early in the nesting cycle.

The time interval between first and second broods was defined as the number of days between fledging of the last young from the first nest and the laying of the first egg in the second nest. If second nests were discovered late in the egg stage or in the fledgling stage, the date of the first egg was estimated by back dating 13 days from the first hatching.

Nest trees were marked with flagging tape after the nest outcome was known. At the completion of the nesting season, distances between successful first nests and subsequent nests by the same individual, and distances between nest failures and subsequent renesting sites were measured.

Our study was designed primarily to track double-brooding but not to provide definitive measures on renesting following failure. Researchers from other areas reported that Wood Thrushes with a successful first nest tended to remain in the same area for subsequent nestings that season (Roth and Johnson 1993, Weinberg and Roth 1998). We hoped to trace such individuals throughout the nesting cycle to determine their double-broodedness. We were less confident of following birds that failed on their first attempt because these individuals often abandon a site after nest failure (Weinberg and Roth 1998). Such transients may renest in other woodlots but time and effort considerations dictated that birds disappearing from our study sites could not be monitored for further nesting attempts.

Statistical methods.—A standard χ^2 (Sokol and Rohlf 1981) was used to examine differences in the rates of double-brooding between years. We used a Student's *t*-test, which assumed unequal variances, to compare the distance between first and second brood nests with the distance between failed nests and the subsequent renesting. Analyses were performed using Microsoft Excel 2000 for Windows.

RESULTS

We banded 70 females at nests where eggs were initiated by 20 June, with 47 of the nests fledging host young. Successful nests were spread fairly evenly between the two study regions, 26 nests in the Waterloo Region and 21 nests on the Escarpment.

Seventy-four percent (n = 35) of females with successful early nests initiated egg-laying

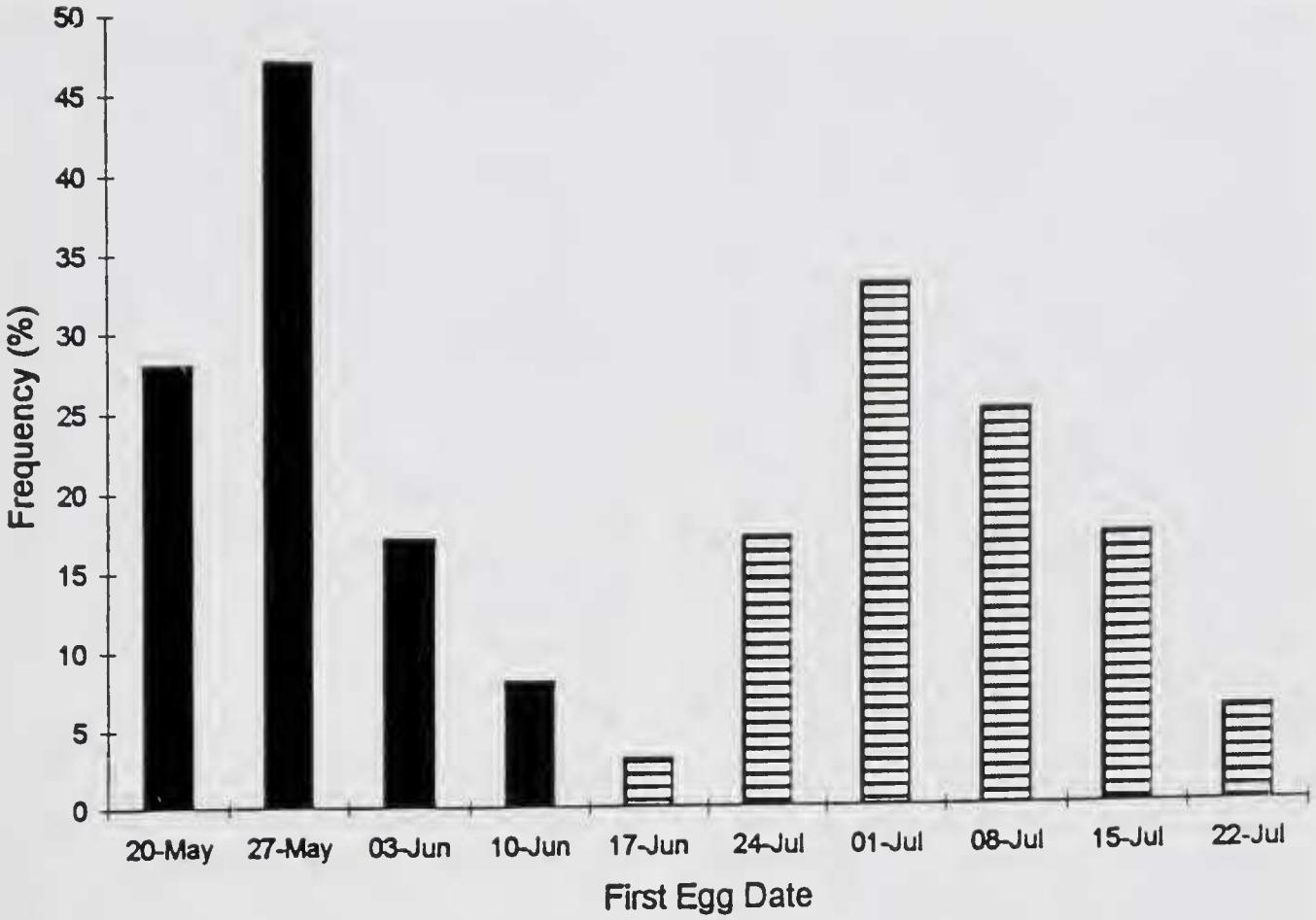

FIG. 1. First egg dates for the first (shaded) and second (striped) nests of double-brooded females.

in a subsequent nest. There was no significant difference ($\chi^2 = 3.08$, 1 df, $P > 0.05$) in the proportion of double-brooding between years: 64% ($n = 16$) in 1998 and 86% ($n = 19$) in 1999. The proportion of double-brooding was similar in each study area; 73% in Waterloo Region versus 76% on the Escarpment. Overall, 36% percent ($n = 25$) of females banded in the early part of the breeding season successfully fledged two broods. There was no evidence of triple-brooding, i.e., two successful broods followed by a subsequent nesting. Two females fledged a first brood and each made two unsuccessful attempts to fledge second broods. We found no evidence of renesting for 13% ($n = 6$) of females following successful early nestings.

The average distance of a second nest from a successful early nest was 72.6 m (±73.6, range 0–400 m with one female reusing her first nest). Half of all second nests (51%, $n = 18$) were built within 50 m of the first nest. Eight females (23%) moved 100–400 m for their second-brood nests. The farthest distance a female dispersed was 400 m to a site across a paved highway. All other double-brooded females remained in the same woodlot for their subsequent nesting attempt.

Average first egg dates in the first successful nests of double-brooded birds was May 24 (±6.4 days, range 13 May to 7 June; Fig. 1); average first egg dates for second-brood nests was 1 July (±7.9 days, range 13 June to 16 July). First eggs of second broods were laid on average 13.4 days (±5.8, range 7–31 days) after the young had fledged from the first nest.

Sixty-five percent ($n = 15$) of unsuccessful females were not encountered after the failure of their early nests. Thirty-five percent ($n = 8$) of unsuccessful females renested on site after failure of their early nests. The average distance of renests from the previous failed nest was 75.8 m (±48.6, range 26–200) which was not significantly different ($t = -0.1805$, 34 df, $P > 0.05$) from the distance between first and second nests.

DISCUSSION

Our results indicate that in southern Ontario, near the northern edge of their breeding

range, most Wood Thrushes with successful early nests were double-brooded. The percentage of birds attempting second broods may have been higher than 74% based on the evidence of 6 later nests containing eggs or young found within 50 m of successful early nests. These nests were depredated or fledged young before the adult females could be captured or identified and were built 1–2 weeks after young were fledged from the earlier nests. Further indication that these were probably second nests comes from the fact that all of the active nests (n = 18) that we subsequently found within 50 m of early successful nests belonged to second-brood females from the first nests. If these 6 nests are included as second-broods, the level of double-brooding over the two years of our study was 87%.

It is likely that despite our best searching efforts some nests were missed, especially in the largest forests, and the frequency of double-brooding might be closer to 100%. Confirmation of second nests in our study regions was complicated by the fact that some double-brooded birds moved considerable distances between nestings. Eight females (23%) dispersed more than 100 m after successful first nests. By contrast, the average distance between nestings in a 15 ha fragment in Delaware was 38 m (±49.2; Roth et al. 1996). It may be that some of the six females that were not encountered after successful early nestings dispersed beyond our study areas for subsequent nestings. Radio telemetry techniques are probably the only effective method to adequately verify double-brooding in populations residing in large forests.

At least 35% of banded females that experienced nesting failure remained on site for another nesting effort. Our renesting data are conservative estimates, however, because we might have missed predated first nests of double-brooded females. It is also possible that we overlooked some later renesting efforts or missed renestings that occurred outside our study areas in the large forests. Unsuccessful pairs that remained on our sites traveled about the same average distance between nesting attempts as successful pairs. However, most birds whose nests failed apparently left the study area, a pattern that has been reported for Wood Thrushes elsewhere (Roth and Johnson 1993, Weinberg and Roth 1998).

We did not encounter any instance of early season nesting failure followed by subsequent double-brooding. This observation must be treated cautiously, however, because we might have missed a predated first nest of a double-brooded female; our egg-dates (Fig. 1) indicate that it certainly is possible for a first nesting attempt to fail before 20 May and for a subsequent double-brooding effort to commence before the end of the month. Wood Thrushes farther south than Ontario have additional time during the breeding season to produce two broods following initial failure (Roth et al. 1996). The shorter breeding season may account for the lower overall proportion (36%) of females on our study sites that fledged two broods of young in a year compared to the 51% recorded in Delaware (Roth et al. 1996).

First egg dates of first and second broods suggest two nesting peaks for southern Ontario Wood Thrushes around 24 June and 1 July; the peaks are about a week later than those reported for double-brooded birds from Delaware (Roth et al. 1996). The average time interval of 2 weeks between first and second broods in Ontario is similar to what has been reported for southerly populations (Brackbill 1943, Longcore and Jones 1969, Roth et al. 1996).

Additional studies are needed to determine whether the frequency of double-brooding in southern Ontario is true for other northerly populations of Wood Thrushes. Further investigation is needed to determine whether within-season dispersal commonly occurs amongst females and, if so, the reasons for such movement. More information is also needed on the frequency of renesting following early-season failure and on the movement of birds that have experienced failure.

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